The effect of prey diet on the feeding preference of *Galendromus occidentalis* (Acarina: Phytoseiidae) for *Tetranychus pacificus* and *Eotetranychus willamettei* (Acarina: Tetranychidae)

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Abstract   The Willamette spider mite (WSM)**,** *Eotetranychus willamettei* (McGregor) and the more damaging Pacific spider mite (PSM), *Tetranychus pacificus* (McGregor) are common pests in vineyards throughout the San Joaquin valley, California. *Galendromus occidentalis* (Nesbitt), a phytoseiid predator also known as the Western predatory mite (WPM), is used to suppress spider mite populations and has been identified as a more effective biological control agent for PSM than WSM. The objective of this study was to determine whether possible nutritional quality differences between PSM and WSM, evaluated through a comparison of the predator's partial life history on the two spider mites, can account for WPM's feeding preference for PSM. The development and fecundity results reveal that WPM's feeding preference is not a result of host quality differences in this system and that WPM, in theory, is a suitable biological control agent for PSM and WSM. The implications of this finding and other possible reasons for the apparent preference of WPM for PSM in vineyards are discussed.

Introduction

Biological control is the use of natural enemies to control unwanted organisms. Worldwide, predatory mites from the family Phytoseiidae have been used as biological control agents for spider mites (Tetranychidae) (McMurtry and Croft 1997). In California, the Pacific spider mite (PSM), *Tetranychus pacificus*, and the Willamette spider mite (WSM), *Eotetranychus willamettei* are of special concern for causing damage in grape vineyards (UC DANR 1992). Leaf feeding by the two species reduces photosynthesis, which may be related to observed decreases in grape quality and sugar concentration; ultimately translating into economic losses (Flaherty and Huffaker 1970, Welter 1989). Comparatively, PSM causes more damage to grape plants than WSM in warmer areas like the San Joaquin Valley. The most important agent for biological control of these two spider mites and other spider mites in general is a phytoseiid predator known as the Western predatory mite (WPM), *Galendromus occidentalis* (Hanna and Wilson 1991, McMurtry and Croft 1997). Huffaker's (1970) field observations indicate that WPM controls PSM better than WSM, but it is not clear whether this is due to the innate or conditioned selectivity of the predator or the influence of a prey characteristic. This information would be useful in understanding phytoseiid behavior and ascertaining the role of WPM as an effective biological control agent for PSM and WSM.

There is little certainty regarding which factors are primarily responsible for inducing preference. Ultimately, what the predator will end up eating is not solely dependent on its foraging behavior. The prey must also be considered because its behavior or life history strategies (e.g. aggregation patterns, dispersal patterns) modulate the type and frequency of the stimulation the predator receives (see Halle and Sabelis 1985a, 1985b). In this sense, preference is the product of the interplay of multiple factors. The tools the predator has for receiving information from the environment and predator-prey dynamics determine what the predator will find and choose. Mites in general, are equipped with sense organs (e.g. mechanoreceptors, chemoreceptors) to help them detect mechanical, chemical, and thermal changes in their environment (Evans 1992). WPM, a blind species exhibiting a non-random searching behavior (Hoy Smilanick 1981), can rely on these receptors to locate prey. However, the predator may rely more on one type of stimulation than another. Thus, to determine the contribution of factors associated with the prey or predator towards preference requires that each be studied separately.

Huffaker's (1970) results suggest that WPM has a feeding preference for PSM over WSM but we need to discover the nature of this non-random selection. Does the predatory mite develop better on PSM or is the mere distribution of PSM responsible for somehow making it more susceptible to predation than WSM? The multiple factors that may be involved have generated various ways of assessing predator preference. Some researchers have studied chemical preference (Sabelis and Van De Baan 1983, Dicke et. al. 1988), preference when different spider mite species are present on the leaves (Hoy and Smilanick 1981), while others have looked at the choice predatory mites make at various prey densities (see Sabelis 1990a; Hanna and Wilson 1991). Another approach is to examine the development of the predator as it feeds on different prey diets. This method reflects the theory of reproductive success (Dicke 1990), which hypothesizes that the predatory mite will prefer the prey which enhances its fitness. The assumption underlying this hypothesis is that host differences affect the development of the predatory mite. The predator needs energy to stay alive and reproduce and if the prey is nutritionally deficient, the predator will starve and produce fewer offspring than it is capable of when satiated (Halle and Sabelis 1985b). Prey variation would be one of the factors responsible for molding predatory mite life history patterns (see Sabelis 1990b). Those that select the most nutritious prey will have a reproductive advantage. Evidence for maximized fitness could be detected by measuring certain predator life history parameters on different prey diets.

To determine whether host quality difference in PSM and WSM can account can account for WPM's feeding preference I examine some of its life history parameters (immature development, fecundity, pre-oviposition period, sex ratio, and survivorship) as it feeds on these two spider mite species. I hypothesize that WPM's enhanced development on PSM, due to a greater host quality over WSM, could be the proximate explanation of WPM's control of PSM in vineyards.

Methods

The mites used in this study, WPM, PSM, and WSM were obtained from cultures raised at the Oxford Tract, UC Berkeley, CA. Chardonnay grape plants used in all components of these experiments were obtained from a campus nursery and kept in a greenhouse. Spider mites were collected from vineyards in Lodi, California and reared on Chardonnay grape plants since the

summer of 2005. In addition, another culture of Pacific mites was reared on bean plants and used as a source of Pacific mite females to supplement those on grape plants. A couple of days before the start of the experiments, WPM reared on two-spotted spider mites (*Tetranychus urticae* Koch) on bean leaves were purchased commercially (Sterling Insectary, McFarland, CA.) and placed on the flat bottom surface of a plastic container lined with wax. Thereafter, WPM were reared on Pacific mites collected from bean plants.

Developmental Study To determine whether WPM's development, pre-ovipostion period, fecundity, sex ratio, and survivorship vary significantly when feeding on different spider mite species, individual WPM mites were subjected to one of two treatments: 1. Leaf disks infested with PSM and 2. Leaf disks infested with WSM. At the start of the study, there were 60 replicates for each treatment. Leaf disks, approximately three centimeters in diameter, were cut from Chardonnay grape leaves using a metal cylinder. Two days prior to addition of WPM eggs to the leaf disks, five female PSM or WSM were added to the leaf disks using a fine brush. This was done to provide spider mites with enough time to lays eggs on leaf disks that would serve as food supply for emerging WPM larvae. To standardize for the age of WPM eggs, Chardonnay leaves were inoculated with WPM females and left in a chamber at 28°C, 40% RH and 16L:8D photoperiod for approximately 12.5 hours. Individual WPM eggs, 0-12.5 hours old, were added to all of the leaf disks using a fine brush. Each leaf disk was placed in a small plastic container filled with 0.05% agar in a chamber at 28°C, 40% RH and 16L:8D photoperiod. Leaf disk size was later reduced to a 15 mm diameter to facilitate finding the predator.

Having added WPM eggs to all of the leaf disks, two observations (approximately 12 hours apart) of each mite's development were made daily until all WPM reached adulthood. The life cycle of WPM is as follows: egg, larva, protonymph, deutonymph, and adult. Changes in life stages from larva to adulthood can be confirmed by the presence of exuvia that WPM leaves behind as it completes each stage. The date and time of each life-stage change was recorded. Experimental WPM females were provided with males immediately or 12 hours after emergence for both treatments (Uncertainty in the sex of the mites caused the delay of male addition. However, because in nature females may not have immediate access to males and there may be a period of female maturation even after mating, this delay most likely has little effect on fecundity). When all of the WPM mites entered adulthood, leafs disk were observed once per day. The presence of experimental WPM adults and the number of eggs laid by experimental

WPM female were recorded. Any missing WPM male provided to experimental WPM females was typically replaced at the time of the next observation. In general, leaf disks were changed every 4-6 days or when observed to be in poor condition. Furthermore, to ensure a constant supply of food for WPM and control for variation resulting from starvation, spider mites of all stages of development were brushed onto the experimental leaf disks regularly. To obtain survivorship data, all WPM mites were observed until they died.   Data for time taken to reach adulthood was analyzed with a two-way ANOVA. Total fecundity, rate of oviposition, pre-oviposition period and sex ratios were analyzed with a one-way ANOVA. Data for total fecundity, pre-oviposition period, and sex ratios were square-root transformed to achieve a normal distribution. Survivorship data did not show a normal distribution even after using different transformations (e.g. log, square-root); therefore, the data was analyzed with the Wilcoxon rank sum test.

Results

    Data for total survivorship were only compared between WPM females because most of the WPM males died of unnatural causes or escaped. There were no significant differences in total fecundity (P=0.28), oviposition rate (P=0.53), sex ratio (P=0.76), development from eggs to adults (P=0.41), or survivorship (P=0.59) between the different diet treatments (Table 1). However, the pre-oviposition period is significantly shorter for WPM females feeding on PSM (P=0.03, Table 1).

Table 1. Effect of PSM and WSM diet on life history parameters of WPM at 28°C.

	No. of WPM for each treatment (PSM,WSM)	PSM[1]	WSM[1]	P-value
Total fecundity (eggs/female)	15, 7	30±14.3	22.1±9.9	0.28
Oviposition rate (eggs/female/day)	15, 7	2.4±0.6	2.2±1	0.53
Pre-oviposition period (days)	23, 18	1.1±0.3	1.6±1	0.03*
Sex ratio (♀:♂)	15, 7	2.0±0.8:1	2.1±0.8:1	0.76
Development time (days egg-adult)	50, 54	4.5±0.4	4.4±0.3	0.41
Survivorship (days)	16, 7	17.5	19.4	0.59

1. Standard deviations are not included for data that did not have a normal distribution (survivorship). For data that were transformed (total fecundity, pre-oviposition period, sex ratios), the averages and standard deviations of the original data are given.

Discussion

The goal of this experiment was to determine if WPM's feeding preference for the more destructive PSM over WSM was a result of nutritional differences between these two spider mites. The results for development study show that there are no differences in most of the life history traits of WPM while feeding on PSM and WSM. The only difference was that the pre-oviposition period of WPM is significantly shorter while feeding on PSM. However, this does not suggest that WPM would have a feeding preference for PSM. WSM and PSM belong to the same family (*Tetranychidae*) and they might not be nutritionally different enough to cause a significant change in the development of the predator. Supporting this are the results obtained for the life history parameters of WPM while raised on two other tetranychid species (Pruszynski and Cone 1973, Tanigoshi et. al. 1975). At 29°C (35-65%RH and 16-h photoperiod), Tanigoshi et. al. (1975) determined the average values for the life history parameters of WPM feeding on *Tetranychus mcdanieli* McGregor: Total fecundity was 28.23 eggs/female, oviposition rate was 2.44 eggs/day, sex ratio (♀:♂) was 2.1:1, and development time (egg-adult) was 7.40 days. At 30°C, Pruszynski and Cone (1973) observed the following for the life history parameters of WPM feeding on *Tetranychus urticae* Koch: Total fecundity was 28.2 eggs/female, oviposition rate was 2.6 eggs/day, pre-oviposition period was 1 day, development time (egg-adult) was 4.5 days, and survivorship was 16.7 days. These data are in the same range of values that I obtained for WPM on PSM and WSM (Table 1) and slight variations are most likely due to temperature differences.

The theory of reproductive success predicts that WPM will prefer the prey that enhances its fitness. Over evolutionary time, the alleles that encoded for the behavior of the predatory mite to choose the mite which maximized its fitness would have increased in frequency in the population. Even though specific preference for a particular prey may not be hardwired in the genetic code of the predator (innate preference), its ability to learn which mite is most nutritious (conditioned preference) may be one of the results of natural selection. In this case, both prey species conferred the same reproductive potential to WPM, indicating that both prey are equally nutritious to the predator. On the basis of developmental data, natural selection could not have caused the innate or conditioned preference of the predator as a result of host nutritional differences in this system. However, this does not imply that other prey characteristics are not involved in molding predator feeding preference. Since we carried out these experiments in the

laboratory, we filtered the effect that other factors would have on preference in the field. For example, to control for starvation the predators in this study were provided with an ample prey supply and only had to search a small area of a grape leaf before coming across a host. In the field however, the predator has to cover larger distances and a patchy distribution of prey colonies in variable weather (Halle and Sabelis 1985 1b). The predator has to cope with food shortages and has to adapt to a mixture of variable conditions that together may influence predator searching and selection.

Even though the theory of reproductive success may not apply in this system, something has to be responsible for the apparent feeding preference WPM has for PSM in vineyards. The lack of developmental differences between the treatments suggests that WPM would provide the same biological control effectiveness for PSM and WSM. This is at odds with Huffaker's (1970) observations that indicated that WPM was more effective at controlling PSM than WSM. The proximate explanation for predator preference in this system is prey aggregation. Hanna and Wilson (1991), using PSM and WSM, have shown that the WPM tends to prefer the most aggregated mite which tended to be PSM. When the abundance levels were varied, WPM had a significant preference for the most abundant mite, regardless of the species. This is a prime example of how life history strategies and prey colonization patterns of may influence the final choice of the predator. Aggregation plays a role in predator selection but the significance of other factors such as prey chemical cues or predator killing efficiency remains to be explored. Some factors, like host quality, may not play an important role for the feeding preference of WPM for PSM and WSM. This shows that preference cannot be assessed in a straightforward fashion by simply studying one factor. There are many components and each one has to be evaluated independently. Complementing what is now known with results from future research will help answer the question surrounding the cause of predatory mite preference.

Acknowledgements

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